

THE FOSSIL FISHES FROM THE SIERRA MADRE FORMATION, OCOZOCOAUTLA, CHIAPAS, SOUTHERN MEXICO

Jesús Alvarado-Ortega, Ernesto Ovalles-Damián, and Alberto Blanco-Piñón

ABSTRACT

Recently, the diverse fossil assemblage discovered in El Espinal and El Chango quarries, near Ocozocoautla de Espinosa, Chiapas, southeastern Mexico, has called the attention of Mexican Paleontologists. The dolomite limestone and fossil bearing strata exploited in these two quarries belong to the Sierra Madre Formation (Aptian?-Santonian). This fossil assemblage involves an increasing number of well-preserved fishes, including an unnamed pycnodontiform, Macrosemiids (*Macrosemiocotzus* sp.), Clupeomorphs (*Triplomystus applegatei* and *Paraclupea*-like specimens), an unnamed ichthyodectoid, Alepisauriformes (*Saurorhamphus* sp., and *Enchodus* sp.), an unnamed gonorynchid, and other unidentified forms. The previously suggested Albian age for El Espinal and El Chango outcrops is questionable, based on the similarity between this Mexican fish assemblage and other well-documented assemblages from Cenomanian localities of the Middle East (i.e., Ein-Yabrud, Namoura) and Eastern Europe (i.e., Comen).

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KEY WORDS: Cretaceous, Cenomanian, fossil, Osteichthyans, Chiapas, Mexico

INTRODUCTION

Since 1980, the number of reports on Cretaceous fish localities from Mexico has been growing steadily (Alvarado-Ortega et al. 2006b). The better known of these are: Tlayúa (Albian) in Puebla; Vallecillo (Turonian) in Nuevo León; at least five locali-

ties around Múzquiz (Turonian-Coniacian) in Coahuila; Xilitla (Turonian) in San Luis Potosí; Muhi (Albian-Cenomanian) in Hidalgo; and localities belonging to the Mexcala Formation (Turonian-Maastrichthian), Guerrero. Here we deal with the fish assemblage from two localities, El Espinal and

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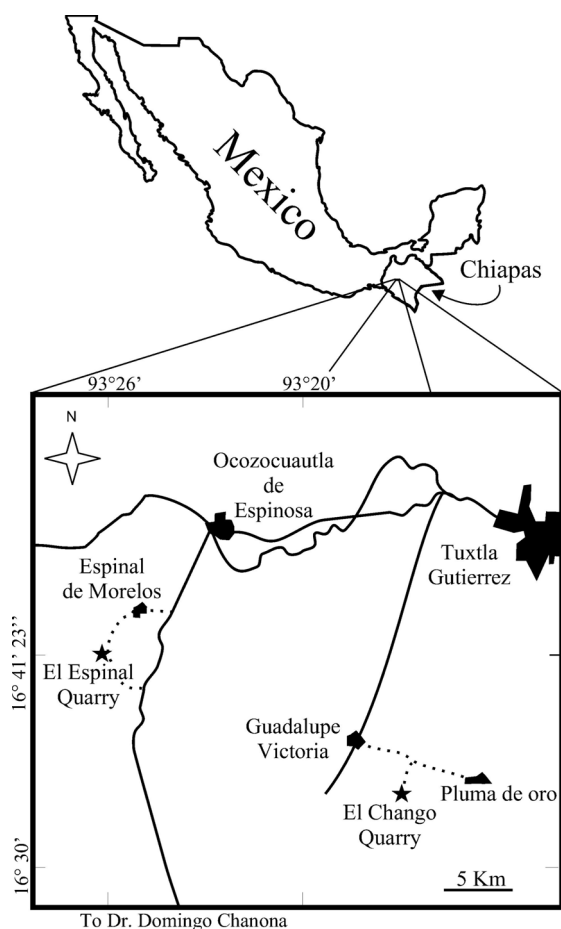


FIGURE 1. Map of El Espinal and El Chango quarries, near Ocozocauatla de Espinosa, Chiapas, Southern Mexico.

El Chango quarries, which are located near Ocozocauatla de Espinosa, Chiapas, southeastern Mexico (Figures 1, 2).

El Espinal quarry is located at N 16°41'1" and W 93°26'97". Although it has been exploited since the 1950s, its fossils began to be systematically collected and studied just until recently (see Ovalles-Damián and Alvarado-Ortega 2002; Ovalles-Damián 2004; Vega et al. 2006; Alvarado-Ortega and Ovalles Damián 2008). The El Chango quarry is located at N 16°34'14" and W 93°16'11" and little information regarding the advances on the study of its fossils have been published (see Ovalles-Damián et al. 2006; Vega et al. 2007).

In the first work on fossils from El Espinal quarry, Ovalles-Damián and Alvarado-Ortega (2002) suggested an Aptian age for this locality based on the occurrence of a paraclupeid fish (here referred as *Paraclupea*-like) similar to *Paraclupea* Sun 1956 from the Aptian freshwater depos-

its of China. Soon after, Vega et al. (2006, 2007), based on invertebrates from El Espinal and El Chango outcrops, supported this same age for these localities; in addition, they suggested that these deposits had been accumulated within a shallow lagoon or estuary with occasional freshwater influence.

The fossils so far collected in the Espinal and El Chango quarries include different fish taxa, plant remains, mollusks, crustaceans, and insects. The fishes known from these Mexican localities show close affinities with those from Cenomanian assemblages located along the Middle East and Eastern Europe (D'Erasmus 1946; Arambourg 1954; Forey et al. 2003; among others). Thus, the fish faunas described herein are an outstanding discovery for Mexico and the entire American continent, demonstrating for the first time the close affinities among Cenomanian fish assemblages in opposite Eastern-Western extremes of the Tethys Sea.

Detailed descriptive works on fishes and other fossils from El Chango and El Espinal localities are still under preparation (except *Triplomystus applegatei* Alvarado-Ortega and Ovalles-Damián 2008) and certainly will require additional effort in the fossil collection and preparation. Therefore, the aim of the present paper is to provide a preliminary description of these fishes in order to contribute to better comprehensive studies on the systematics, phylogeny, and biogeography of fossil fishes.

The fossil bearing strata at El Espinal and El Chango quarries constitute at least 3 meters of a monotonous dolomitic carbonate sequence. Unfortunately, the bottom and top of this sequence remain unknown. The thickness of the strata ranges from a few millimeters to about 15 centimeters. The strata show a light brown to yellowish color and parallel lamination. Occasionally, orange layers 1mm thick of iron oxides are exposed within the carbonate strata. Toward the top of the sequence (the last 30 centimeters), the carbonates alternate with clayish material, which could be a consequence of the dissolution during soil formation (Figure 2).

The strata exposed in El Chango and El Espinal have been assigned to the Sierra Madre Formation under the criteria of their geographic distribution within the Ocozocauatla area; however, at this moment the total thickness and lateral boundaries of these strata remain unknown. Besides, the present lithological description of these localities does not match with any of the 11 lithological units of the Sierra Madre Formation

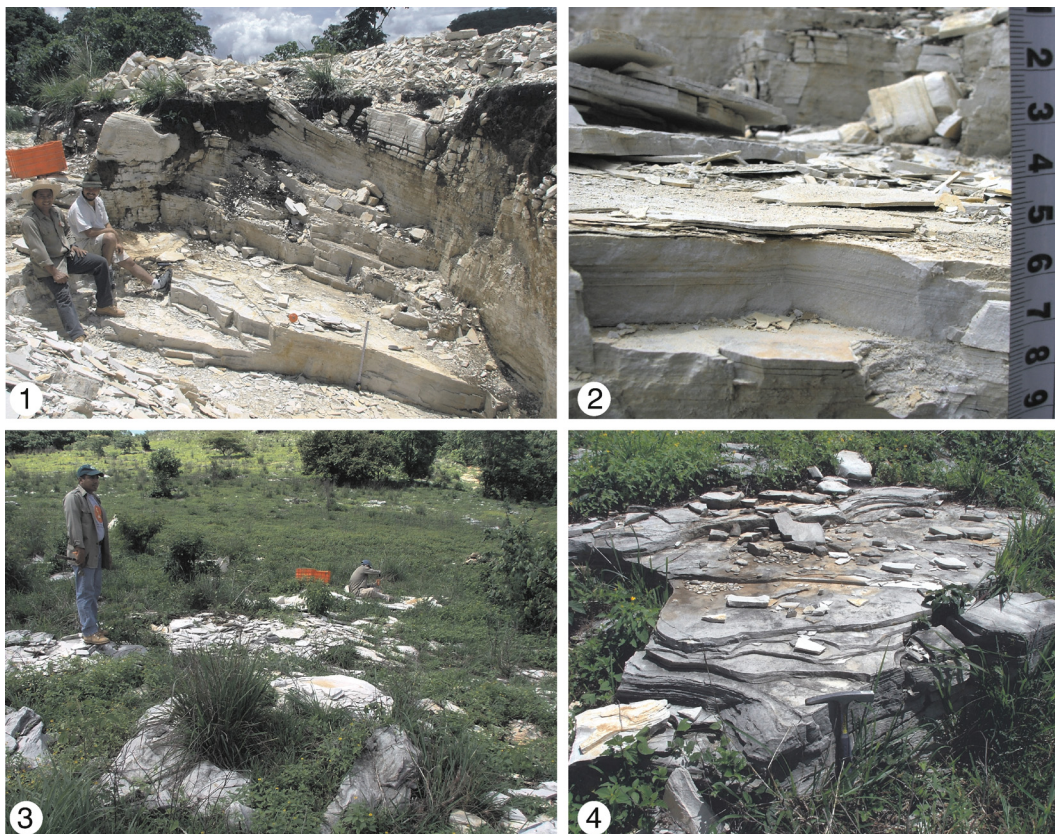


FIGURE 2. Fossiliferous outcrops of laminated dolomitic limestones in the lower section of the Sierra Madre Formation, near Ocozocoautla de Espinosa, Chiapas, southern Mexico. 1 and 2, El Espinal Quarry, a general view and strata details respectively. 3 and 4, El Chango quarry, a general view and strata details.

described by Steele (1986), so at this moment, there are not enough data to support a possible lithostratigraphic relationship between both localities and the units of the Sierra Madre Formation. In addition, the absences of detailed biostratigraphic studies along with the lack of index fossils do not allow a certain age assignation of El Espinal and El Chango strata; for that reason, their precise temporal relationships within the Sierra Madre Formation are imprecise, too.

The specimens referred here are housed in the Museo de Paleontología “Eliseo Palacios Aguilera” (IHNFG), the Instituto Nacional de Antropología e Historia (INAH), and the Museo de Paleontología at Facultad de Ciencias, Universidad Nacional Autónoma de México (FCMP).

SYSTEMATIC PALEONTOLOGY

Order Pycnodontiformes Berg, 1937
 Family Pycnodontidae Agassiz, 1833
 Genus and species unnamed

Material examined. FCMP 00/497, a complete and articulated fish from El Espinal quarry preserved as the impression of its left lateral side (Figure 3.1, 3.2).

Description. This is a drop-shaped and prognath fish with total length (TL) and standard length (SL) equal to 255 and 195 mm, respectively. The maximum body depth is about 58 % of SL. The head length is about 38 % of SL. The dorsal and anal fins rise at 64 and 70 % of SL, respectively. The pelvic fin is opposed to the origin of the dorsal fin (Figure 3.1).

The skull of this fish shows a well-defined parietal process and a dermocranial fenestra bordered by the frontal, parietal, and dermal supraoccipital bones (Figure 3.2). The details of both jaws

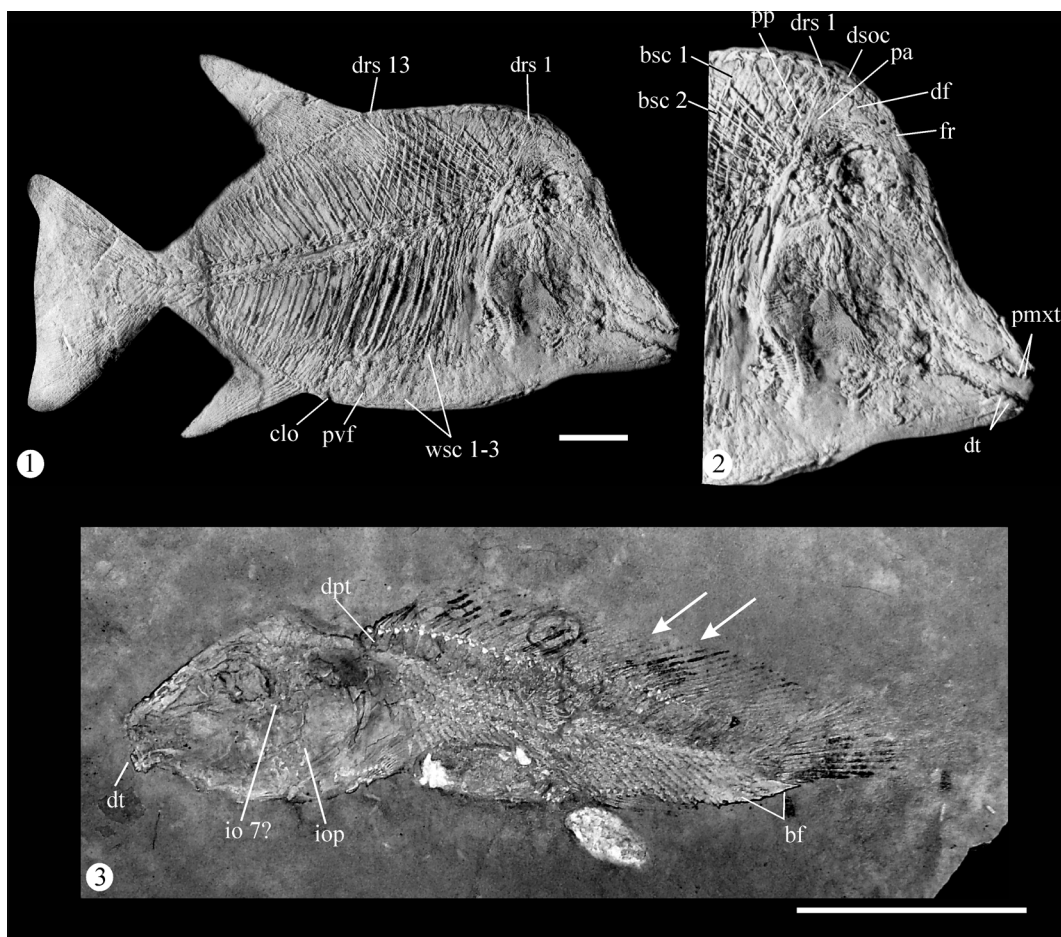


FIGURE 3. Non-teleostean fishes from Sierra Madre Formation. 1, Silicone peel of FCMP 00/497, a pycnodontid fish from El Espinal quarry. 2, Close-up of the head of FCMP 00/497. 3, IHNFG 2981, *Macrosemiocotzus* sp. from El Espinal quarry. Abbreviations: bf, basal fulcra; bsc 1-2, bar-like scales (rows 1-2). clo, cloaca; df, democraneal fenestra; dpt, dorsal pterygiophore; drs 1-13, dorsal ridge scales; dsoc, dermal supraoccipital; dt, dentary teeth; fr, frontal; pa, parietal; pmxt, premaxilla teeth; io 7, infraorbital seven; iop, interopercle; pp, parietal process; pvf, pelvic fin; wsc 1-3, wide scales (rows 1-3); arrows in 3 show the different length of the dorsal rays. Scale bars equal 25 mm.

are not well preserved; nevertheless, it is possible to notice two incisiform teeth in the premaxilla and another two in the anterior dentary end. Only some stout crushing teeth are preserved in the vomer and prearticular.

Regarding the criteria suggested by Poyato-Ariza and Wenz (2002, p. 118, figures 34, 36), the shape of the anal and dorsal fins of FCMP 00/497 is falcate [the rays (*lepidotrichia sensu* Poyato-Ariza and Wenz 2002), i.e., the prominent and triangular anterior sections of these fins are at least twice as long as the posterior ones], and the caudal fin shape is double emarginated (Figure 3.1).

The body of this fish is not covered by scales except in the area in front of the anal and dorsal fins (Figure 3.1). Three rows of flat, wide, and triangular-rhomboidal scales cover the ventral and mid-

dle part of the abdominal area, and probably four rows of stout bar-like scales cover the remaining abdominal area and all the area between the occiput and the dorsal fin. Some ridges ornament the external surfaces of the scales on the abdominal area.

Thirteen smooth and triangular dorsal ridge scales cover the anterior dorsal border of the body, between the occiput and the dorsal fin. These dorsal ridge scales, except the anterior one, are regular in size. The anterior one is about twice as large as the following posterior ones. Each of these scales shows a middle posterior sharp protuberance connected to a middle anterior notch of the next posterior scale. The maximum depth of the body is located just in the back of the occiput. The

TABLE 1. Comparison among pycnodontids with dermocraneal fenestra (based on Applegate 1992; Poyato-Ariza and Wenz 2002; Machado and Brito 2006). Gray areas show shared characters of FCMP 00/497 and other genera.

	<i>Potiguara</i>	<i>Tepexichthys</i>	<i>Ocleodus</i>	<i>Oropycnodus</i>	<i>Pycnodus</i>	FCMP 00/497
Body shape	Rhomboidal - diamond				Drop-like	
Dorsal profile	A prominent angle is present				Slightly curved, convex	
Origin of dorsal fin	At the apex of dorsal profile				Behind the apex of dorsal profile	
Size of dorsal ridge scales	All are similar			The anterior one is the largest		
Dorsal ridge scales	12-14?	17	12-14	7-9		13
abdominal Scales	?	Wide and flat		Bar-like		Wide and flat
Incisiform teeth in dentary and premaxilla	?	3	2			
Shape of caudal fin	Straight	Concave	Double margined			

details of the ventral keel scales are obscured due their bad preservation.

Remarks. Poyato-Ariza and Wenz (2002) performed the last comprehensive review on the order Pycnodontiformes. Later Poyato-Ariza and Wenz (2004, 2005), Kriwet (2004), and Machado and Brito (2006) provided additional taxonomical information. The geologic range of this group is Triassic-Eocene, and it involves about 650 nominal species belonging to about 40 genera, 10 of which are based entirely on dental remains (Kriwet 2004). Diversity of Mexican pycnodontiforms includes numerous unnamed taxa from localities within Nuevo León, Coahuila, Hidalgo, San Luis Potosí, Puebla, and Chiapas (Applegate et al. 2004), as well as Guerrero (Garibay-Romero, personal commun., 2006).

Although the complete description of FCMP 00/497 is under preparation, in advance and based on a brief comparative analysis, it can be demonstrated that it represents a new form within the family Pycnodontidae. This fish shows the parietal process (Figure 3.2) that currently represents the only unambiguous synapomorphy of this family (Machado and Brito 2006). Table 1 summarizes comparative characters that support the singularity of FCMP 00/497. Among pycnodontids, the dermocraneal fenestra is present in *Ocleodus* Poyato-Ariza and Wenz 2002; *Oropycnodus* Poyato-Ariza and Wenz 2002; *Pycnodus* Agassiz 1833; *Tepex-*

ichthys Applegate 1992; and *Potiguara* Machado and Brito 2006; as well as FCMP 00/497 (Figure 3.2). In all these nominal genera the body shape is either diamond or rhomboidal, but *Pycnodus* (Lambers 1991, figure 20.1) shows a similar drop-like body shape as FCMP 00/497. In drop-like pycnodonts, the dorsal fin is located behind the highest point of the dorsal outline [the dorsal apex *sensu* Poyato-Ariza and Wenz (2002)]; in contrast, in the other genera listed above, the dorsal fin originates just in this highest point of the body or dorsal apex. In FCMP 00/497 and *Pycnodus*, the dorsal border between the occiput and the dorsal fin is slightly curved and convex; whereas the diamond or rhomboidal pycnodonts have a remarkable dorsal apex forming an acute angle.

Regarding the ossification patterns of pycnodontiform scales described by Poyato-Ariza and Wenz (2004, character 64), it is possible to recognize that FCMP 00/497 and *Pycnodus* differ from other pycnodontids. In FCMP 00/497, as in *Tepexichthys* and *Ocleodus*, the abdominal area shows wide and flat scales (also named as complete ossified scales) and above them there are solid bar-like scales (or incomplete ossified scales) (Figure 3.1). In contrast, all the scales in *Pycnodus* and *Oropycnodus* are solid bar-like. In *Potiguara* the abdominal scales are unknown (Machado and Brito 2006)

Those 13 dorsal ridge scales found in FCMP 00/497 fall within the ranges of *Ocleodus* and prob-

ably *Potiguara* (12-14); in contrast, the dorsal ridge scales are 17 in *Tepexichthys* and 9-7 in *Oropycnodus* and *Pycnodus*. In FCMP 00/497, *Pycnodus*, and *Oropycnodus*, the most anterior dorsal ridge scale is slightly larger than the posterior ones; whereas in *Tepexichthys*, *Ocleodus*, and probably *Potiguara*, all dorsal ridge scales have a similar size (Applegate 1992, p. 171; Poyato-Ariza and Wenz 2004, characters 69 and 71; Machado and Brito 2006, p. 4 and figure 2).

FCMP 00/497 has two incisiform teeth in the premaxilla and dentary, like the rest of the pycnodontid genera with dermocranial fenestra except *Tepexichthys*, which has three incisiform teeth on each of such bones (Applegate 1992; Poyato-Ariza and Wenz 2004). In *Potiguara*, these teeth are unknown (Machado and Brito 2006).

Finally, the caudal fin is double margined in FCMP 00/497 (Figure 3.1), as well as in *Oropycnodus*, *Ocleodus*, and *Pycnodus* (Poyato and Wenz 2002, character 73). In contrast, the caudal fin is concave in *Tepexichthys* and straight in *Potiguara* (Applegate 1992, figure 4; Machado and Brito 2006).

Order Macrosemiiformes Grande and Bemis, 1998
Family Macrosemiidae Thiollière, 1858
Genus *Macrosemiocotzus* González-Rodríguez,
Applegate, and Espinosa-Arrubarrena, 2004
Macrosemiocotzus sp.

Type species – *Macrosemiocotzus americanus* González-Rodríguez, Applegate, and Espinosa-Arrubarrena, 2004; Tlayúa Formation (Cretaceous, Albian), Puebla, Mexico.

Material examined – IHNFG 2981 (Figure 3.3), complete articulated specimen from El Espinal quarry showing its left side.

Description – The skeleton of the specimen is complete and articulated. The total and standard lengths are 93 and 75 mm, respectively. The head length is 23 mm ($\approx 33\%$ of SL). The maximum body depth is about 20 mm ($\approx 26.6\%$ of SL), it is located just in the back of the head and is about two times the depth of the caudal peduncle. The dorsal fin is long and occupies almost all the trunk length. The anal fin is short and includes seven branched rays. The preanal length is 53 mm (70% of SL). Both paired fins are located in the ventral border of the body; the pectoral one is rounded and larger than the pelvic one, which is located in the middle of the trunk. The caudal fin includes 11 branched rays, and its posterior border is rounded (Figure 3.3).

IHNFG 2981 shows a well preserved infraorbital bone located close to the ventral posterior edge of the orbit (probably the seventh within the circumorbital series). The infraorbital is a tube with a small rectangular sheet extended ventrally. This specimen partially preserves the interopercle bone located behind the preopercle and far from the lower jaw. The anterior teeth on the dentary and premaxilla are large, stout, and sharp pointed (Figure 3.3).

The elongated dorsal fin occupies all the back of the body, from the occiput to the caudal fin base, including 36 rays. The first dorsal fin ray is short, unbranched, and unsegmented. The other dorsal rays are almost regular in size (about four times as large as the first one); however, those three or four dorsal fin rays located in the positions 15 and 18 are slightly shorter than those located behind them (see arrows in Figure 3.3). It means that the dorsal fin includes two continuous lobes with 18 rays in each one.

There are 39 or 40 scale rows covering the whole body except in the area along the dorsal fin base. This nude area represents about a quarter of the body deep. All the scales are rhomboidal, and their size decreases progressively in an anterior to posterior order.

Remarks – González-Rodríguez et al. (2002) and González-Rodríguez (2004) identified IHNFG 2981 as *Macrosemius* cf. *M.ourneti* (Thiollère 1850) without any further discussion supporting such identification. Based upon the present description we disagree with that previous study as it is discussed below.

The macrosemiids are a Triassic-Early Cretaceous halecostom group with a constrained geographical distribution that includes localities in Europe and Mexico (Bartram 1977; González-Rodríguez et al. 2004). Recently, Murray et al. (2007) discovered Macrosemiids in Late Cretaceous deposits of Morocco. Apart from the present specimen from Sierra Madre Formation, these fishes are present in America only in the Albian limestones of the Tlayúa Formation (Applegate 1996; González-Rodríguez 2004).

IHNFG 2981 shows two synapomorphies of Macrosemiidae (González-Rodríguez et al. 2004, p. 285-286) supporting its inclusion within this family: 1) Scroll-like shaped infraorbital series (see label io 7? in Figure 3.3); and 2) the location of the interopercle, which is preserved behind the preopercle and far from the lower jaw (see label iop in Figure 3.3).

TABLE 2. Comparison between macrosemiids with incomplete squamation (nude area) along the dorsal fin base (based on Bartram 1977, and González-Rodríguez et al. 2004). Gray areas show characters found in IHNFG 2981 that support its inclusion into *Macrosemiocotzus*. * This area of small scales is located below the posterior part of the dorsal fin.

	<i>Legnognatus</i>	<i>Macosemius</i>	<i>Macrosemiocotzus</i>
Dorsal fin	Short	Long	
Lobes in dorsal fin	1		2
Area of small scales *	Absent	Present	Absent

According to Bartram (1977) and González-Rodríguez et al. (2004, character 8), there are only three genera among macrosemiids with a nude back or an incomplete squamation area along the base of the dorsal fin (in these fossils, the dorsal pterygiophores are exposed because the scales do not cover them): *Legnonotus* Egerton 1854; *Macrosemius* Agassiz 1844; and *Macrosemiocotzus*. Table 2 summarizes a comparison between these three genera. *Legnonotus* has a short dorsal fin that comprises 25 dorsal rays forming a continuous lobe located in the middle of the trunk, far from the occiput and the caudal peduncle (Bartram 1977). In contrast, 30 or more dorsal rays are present in *Macrosemiocotzus* and *Macrosemius* (30-32 and 32-39, respectively). In addition, in these last two genera the dorsal fin occupies almost all the back area.

Besides, *Macrosemiocotzus* has a dorsal fin divided in two continuous lobes (González-Rodríguez et al. 2004), whereas in *Macrosemius* this fin has a single lobe. These two genera also differ from each other because in *Macrosemius* the area below the posterior part of the dorsal fin shows very small scales (Bartram 1977, figure 1), whereas in *Macrosemiocotzus* this area is covered with scales undistinguishable from those on other parts of the body (González-Rodríguez et al. 2004, figure 8). Bartram (1977) described the area with small scales in *Macrosemius* (which represent a diagnostic character of this genus) as the intercalation of primary and secondary scale rows. IHNFG 2981 is recognized as a *Macrosemiocotzus* specimen because it has a long dorsal fin with two continuous lobes and scales with regular size along the whole body (Figure 3.3, Table 2).

Macrosemius is a Jurassic (Kimmeridgian) European fish that includes two species: *M. rostratus*, from Eichstätt and Kelheim, Germany, and *M. fourneti* from Cerin, France (Bartram 1977). In contrast, *Macrosemiocotzus* includes a single species from the Cretaceous (Albian) limestones of the

Tlayúa quarry, Mexico (González-Rodríguez 2004). Comparing these temporal and geographical ranges, the taxonomical recognition of IHNFG 2981 as a *Macrosemiocotzus* specimen increases the geographic range of this genus, which remains as an exclusive Albian-Cenomanian American taxon. At the same time, *Macrosemius* is retained as an exclusive Jurassic European fish.

The small anatomical difference (the amount of dorsal fin rays) noted between *Macrosemiocotzus americanus* (30-32) and the specimen IHNFG 2981 (36), suggests that the latter could represent a new *Macrosemiocotzus* species; however, an extensive comparative study involving these fishes is still required.

Order Ichthyodectiformes Bardack and Sprinkle, 1969

Suborder Ichthyodectoidei Romer, 1966
Genus and species unnamed

Material examined – IHNFG 2985 (Figure 4.1, 4.2), IHNFG 2994 a and b (part and counterpart), and IHNFG 3000; all from El Chango quarry.

Description – IHNFG 2985 preserves the head and the first 33 vertebrae, the length of the head is 75 mm; the length of the remaining section of the spinal column is 200 mm (Figure 4.1, 4.2). IHNFG 2994 is preserved as part and counterpart of the head and 26 disarticulated vertebrae; the head length reaches 70 mm. IHNFG 3000 is a section of the trunk, 120 mm in length, which goes from the pelvic girdle to the anterior part of the dorsal fin, along with 16 vertebrae.

This fish shows the characteristic head of the Cretaceous ichthyodectiforms. In IHNFG 2985, the floor of the nasal capsule shows a well-ossified ethmopalatine, the premaxilla-maxilla attachment involves their complete depth, there is a high and triangular supraoccipital crest, the otic and ocular sections of the parasphenoid form an angle of about 131°, and there is a basal sclerotic bone with serrated margins occupying the orbit (Figure 4.2).

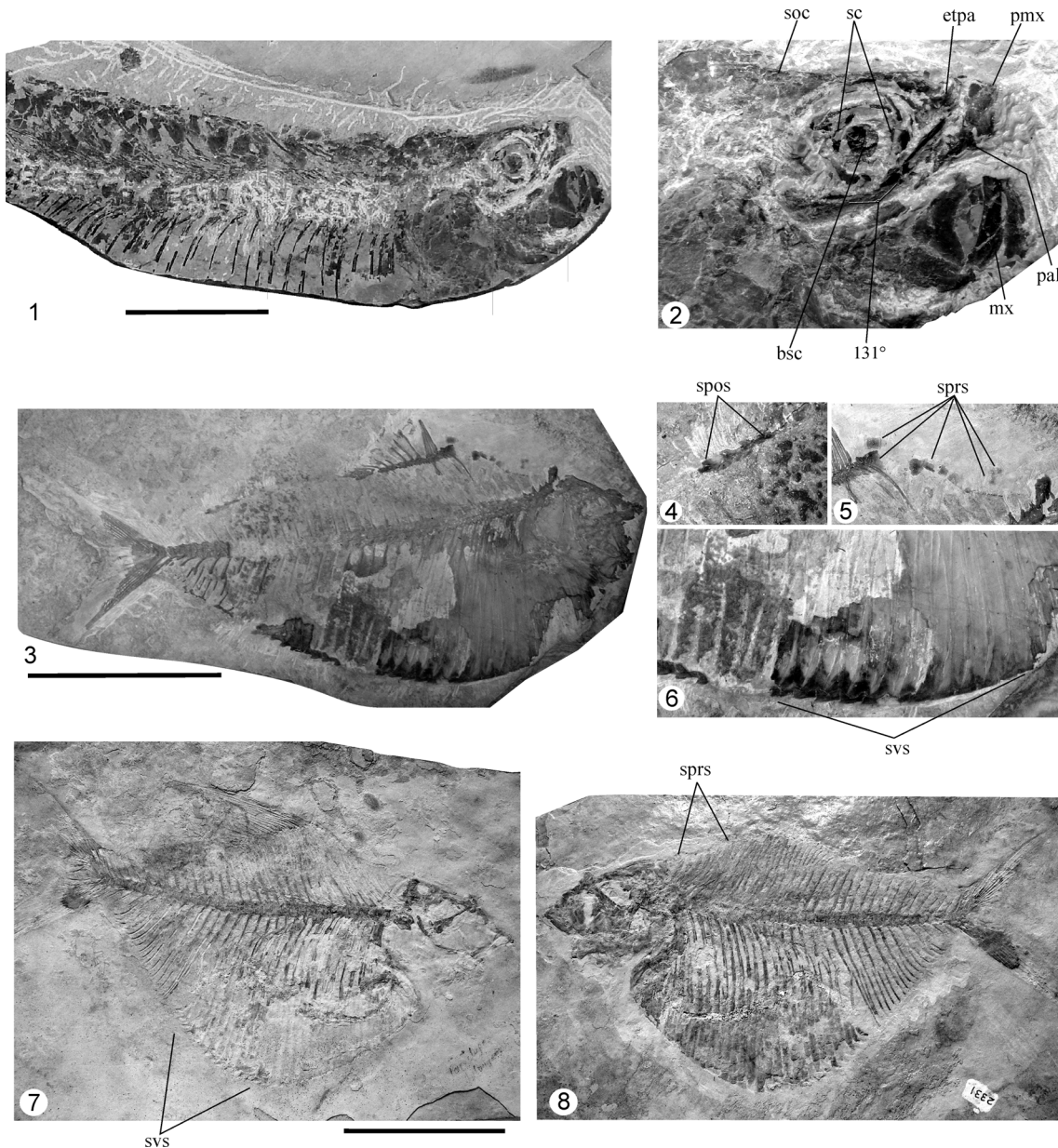


FIGURE 4. Teleostean fishes from Sierra Madre Formation. 1 and 2, IHNFG 2985, an ichthyodectiform fish from El Chango quarry, complete specimen and close-up of the head. 3-6, INAH 1941, *Triplomystus applegatei* from El Espinal quarry, complete specimen and details, close-up of the postdorsal scute series (4), close-up of the predorsal scute series (5), and close-up of the ventral scute series (6). 7 and 8, part and counterpart of IHNFG 2984, *Paraclupea*-like, from el Espinal quarry. Abbreviations: 131°, angle of paraesphenoid; bsc, basal sclerotic bone; etpa, ethmopalatine; mx, maxilla; pal, palatine; pmx, premaxilla; sc, sclerotic; spos, scutes of the postdorsal series; soc, supraoccipital; sprs, scutes of predorsal series; svs, scutes of ventral series. Scale bars equal 50 mm.

In IHNFG 2994, the lower jaw is rectangular with a deep dentary symphysis and a straight alveolar border parallel to its slightly convex ventral border.

In IHNFG 2985, the teeth in the premaxilla and anterior maxilla are regular in size; they are conical, straight, and sharp (Figure 4.2). There are about 20 teeth along the anterior and ventral border of the premaxilla that increase in length from

0.5 mm to about 1 mm. In this specimen, the larger premaxilla teeth are similar to those present in the maxilla.

Pelvic, anal, and dorsal fins are preserved in IHNFG 3000. The anal fin includes at least 28 rays, six of which (the first) form a triangular lobe. The triangular dorsal fin is opposed to the anal fin and located behind its lobe. The distance between the

pelvic and anal fins is equal to that of eight or nine centra. The first rays in the pectoral and pelvic fins are wide and flat.

Remarks – The order Ichthyodectiformes includes Jurassic and Cretaceous fishes characterized by the presence of the ethmopalatine bones occupying the nasal capsule floor, large coracoids meeting each other forming a middle longitudinal symphysis, and uroneurals covering the lateral surfaces of the first preural centra (Patterson and Rosen 1977; Taverne 1986; Maisey 1991). The occurrence of the ethmopalatine bones in the specimens here referred supports their inclusion into the order Ichthyodectiformes (see Figure 4.2).

The suborder Ichthyodectoidei includes all Cretaceous forms so far known plus *Thrissops* Agassiz 1833, a Jurassic European form (see Patterson and Rosen 1977; Stewart 1999; Alvarado-Ortega 2005; among others). Cretaceous taxa within this suborder form a monophyletic group that is characterized by the presence of a rectangular lower jaw and a wide premaxilla-maxilla attachment. These characters are present in the specimens here referred from El Chango quarry supporting their inclusion into this nominal suborder (Figure 4.2).

The interrelationships of ichthyodectiforms remain controversial because there are several forms that still need to be described or redescribed before performing a comprehensive study. However, two crown monophyletic ichthyodectoid families are clearly to be recognized: a) Saurodontidae includes genera with a prognathic lower jaw and an edentulous premaxillary bone (see Stewart 1999); and b) Ichthyodectidae involves genera with a broad parasphenoid angle (149°-160°, formed between the orbital and the otic sections of the parasphenoid) and a hyomandibular fossa laying in parallel to the orbital section of parasphenoid (see Taverne 1986; Blanco-Piñón and Alvarado-Ortega 2007). Because the specimens here referred do not show these diagnostic characters, we are unable to place them within any of these families.

Although we concluded in the previous paragraph that the relatives of the ichthyodectiforms from El Chango must be placed among basal ichthyodectoid taxa, which include well-known fishes as *Unamichthys* Alvarado-Ortega 2004 and *Cladocycclus* Agassiz 1844, as well as a large number of scarcely documented genera, such work is beyond the scope of the present work, and additional research is required to recognize the accurate taxonomical identity of these Mexican fishes.

Prymnetes longiventer Cope 1871 is the other ichthyodectiform known from Chiapas. Unfortunately, this species is represented by a single specimen from an unknown locality near Tuxtla Gutiérrez. The head of this specimen is distorted; therefore all its diagnostic characters are based on the postcranial skeleton (its specific epithet is based on the large number of abdominal vertebrae). Unfortunately, none of the specimens recently collected in El Chango quarry preserves the whole body precluding a better anatomical comparison with *Prymnetes* and other basal Ichthyodectoids.

Order Ellimmichthyiformes Grande, 1985
Family Paraclupeidae Chang and Chou, 1977
Genus *Triplomystus* Forey, Yi, Patterson, and Davis, 2003

Triplomystus applegatei Alvarado-Ortega and Ovalles-Damián, 2008.

Material examined – INAH 1941 from El Espinal quarry, almost a complete specimen exposing the left side (Figure 4.3-4.6).

Remarks A complete description of *Triplomystus applegatei* was performed by Alvarado-Ortega and Ovalles-Damián (2008); relatives of *T. applegatei* were described by Forey et al. (2003) as *T. noorea* and *T. oligoscutatus*. The genus *Triplomystus* includes the so called “triple armored herrings,” that differ from the rest of the Ellimmichthyiforms in their three scute series along the body borders (predorsal, postdorsal, and ventral series) instead of the regular two series (predorsal and ventral) found in other ellimmichthyiforms. The presence of these three scute series in INAH 1941 justified its inclusion within the genus *Triplomystus* (Figure 4.4-4.6). Alvarado-Ortega and Ovalles-Damián (2008) found differences among the three *Triplomystus* species, which reside mainly on the meristic data of the anal and dorsal fins, as well as in the number of scutes that form the predorsal, postdorsal, and ventral series.

Genus and species unnamed
(informally named *Paraclupea*-like)

Material examined – IHNFG 2984 a and b (part and counterpart), a complete fish from El Espinal quarry (Figure 4.7-4.8). IHFG 3002 a and b, part and counterpart of a fish lacking the head from El Chango quarry.

Note – Ovalles-Damián (2004) named the specimen IHNFG 2984 *Paraclupea*-like. Today, E.D.O.

TABLE 3. Comparison among “double armored herring” genera included within the family Paraclupeidae (based on Hay et al. 2007, Alvarado-Ortega et al. 2008). Gray area shows the shared characters.

	Preural vertebrae	Anal fin rays	Dorsal fin rays	Predorsal scutes
<i>Scutatuspinosus</i>	32	9	12	9-11
<i>Ellimmichthys</i>	33-36	10-14	11-14	12-13
<i>“Diplomystus” solignaci</i>	43	15	14	?
<i>Ellimma</i>	36-38	15	14	12-14
<i>Ezkutuberezi</i>	35	23	24	?
<i>Paraclupea-like</i>	34	17	18	18
<i>Paraclupea</i>	39	14-15	18	18
<i>Tychoichthys</i>	38	23	19	16

is working on the formal description of both referred specimens.

Description – Although IHNFG 2984 is a complete articulated fish, the skeleton is partially dissolved (Figure 4). The total and standard lengths of the diamond-shaped specimen are 222 and 165 mm, respectively. The maximum body depth is 115 mm (64.4 % of SL). There are 39 vertebrae along the spinal column, including 14 caudal and 25 abdominal centra. There are two scute series, the ventral and the predorsal. The ventral series includes 42 or 43 wide scutes covering the abdomen, and the predorsal series involves about 18 scutes located in front of the dorsal fin. The size of the predorsal scutes increases in an anterior to posterior order, and they are ornamented with radiating ridges. The dorsal fin includes approximately three unbranched and 21 branched rays that are connected with 19 dorsal pterygiophores. The anal fin rays are not preserved but 16 pterygiophores are present (Ovalles-Damián 2004).

Remarks The order Ellimmichthyiformes is a basal group of clupeomorph fishes named by Grande (1985). In this group, the parietals meet each other along the middle line of the skull, the anterior ceratohial has the beryciform foramen, and subrectangular scutes in the predorsal series. Clupeomorph fishes are characterized by the occurrence of the ventral scute series that form the ventral keel (Grande 1985). Recently, Alvarado-Ortega et al. (2008) suggested that this order includes two families: Paraclupeidae and Sorbinichthyidae. In the paraclupeids the size of the predorsal series increases in an anterior to posterior order, the posteriormost of these scutes show a strong spine. In contrast, the sorbinichthyids are fishes with a large supraoccipital crest, and 20-30 subrectangular

scutes with serrated posterior borders forming the predorsal series. According to Ovalles-Damián (2004), IHNFG 2984 shows about 18 predorsal scutes, whose size increases in an anterior to posterior order; these characters support the inclusion of these fishes into the family Paraclupeidae.

According to Alvarado-Ortega et al. (2008), the family Paraclupeidae comprises the genera: *Scutatuspinosus* Silva-Santos and Correa 1985, from the Early Cretaceous (Neocomian) lacustrine sediments within Recôncavo Basin, Brazil; *Ezkutuberezi* Poyato-Ariza, López-Horgue, and García-Garmilla 2000, from the Early Cretaceous (Valangian-Barremian), deltaic and lacustrine deposits from the Villaro Formation, Spain; *Ellimma* Jordan 1913, from the Early Cretaceous (Aptian-Albian), brackish lagoon and open sea deposits of Riacho Doce, Muribeca Formation, Brazil; *Ellimmichthys* Cope 1886, from the Early Cretaceous (Hauterivian-Barremian) estuarine deposits of the Marfim Formation, Brazil, and the Early Cretaceous (Aptian-Albian) freshwater deposits of the Cocabeach Series, Equatorial (Spanish) Guinea, Central Africa; *Paraclupea* Sun 1956, from the Lower Cretaceous probable freshwater deposits of the Chawan Formation, China; as well as *Triplomystus* (see above) and the species *“Diplomystus” solignaci* Gaudant and Gaudant 1971, from the Late Cretaceous (Senonian) marine sediments at Calcaires rosés de Gabès, Gouvernorat de Gabès, Tunisia. *Tychoichthys dunveganensis* Hay, Cum-baa, Murray, and Plint 2007, was recently described based on a single specimen from the Late Cretaceous (Cenomanian) Marine mudstone of the Dunvegan Formation, Canada; based on its description it is recognized as a paraclupeid fish. *Triplomystus* has three scute series (see the ante-

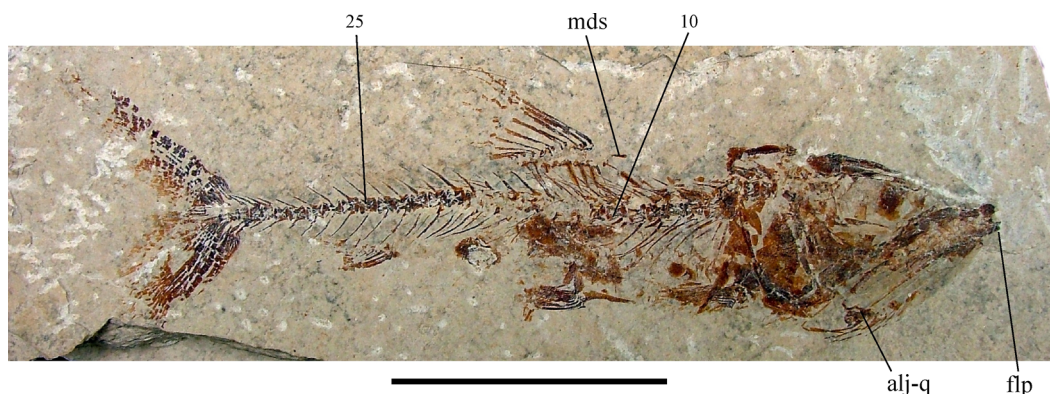


FIGURE 5. IHNFG 2987, *Enchodus* sp. from El Chango quarry. Abbreviations: alj-q, articulation of lower jaw with quadrate; flp, finger-like processes on dentary; mds, mid-dorsal scale, numbers on the vertebrae show the position of each centra. Scale bar equals 25 mm.

rior section above), therefore it was named a “triple armored herring”; in contrast, the rest of the Ellimichthyiformes present only two scute series (the predorsal and ventral series) and are commonly known as “double armored herrings.”

Table 3 summarizes the following comparative analysis among the “double armored herrings” genera included in the family Paraclupeidae (see Zaragüeta-Bagils 2004; Hay et al. 2007; Alvarado-Ortega et al. 2008). These fishes are relatively easily distinguishable from each other because of the scutes that form the predorsal series, the rays involved within the impaired fins, and the preural vertebrae. However, Ovalles-Damián (2004) noted that IHNFG 2984 represents a new genus and species because such accounts do not match with those found in other paraclupeids, he suggested that his *Paraclupea*-like fish is closer to *Paraclupea* than to any other paraclupeid.

Order Alepisauriformes *sensu* Regan, 1911
 Suborder Enchodontoidei *sensu* Goody, 1969
 Family Enchodontidae *sensu* Goody, 1969
 Genus *Enchodus* Agassiz, 1835
Enchodus sp.

Type species: *Enchodus lewesiensis* (Mantell 1822), from the Chalk of Sussex, Cenomanian-Campanian, England.

Material examined – IHNFG 2987 (Figure 5), IHNFG 2988, IHNFG 3004 a and b, and IHNFG 3005; all from El Chango quarry.

Description – IHNFG 2987 (Figure 5) is the only complete specimen so far known. Its total and standard lengths are 110 and 88 mm, respectively. Its head length is 32 mm (36.3 % of SL). Its predorsal length is 44 mm (50 % of SL). Its preanal length is 68 mm (77.3 % of SL). The lower jaw is strong

and triangular, higher in the posterior region where its joint with the quadrate is exposed. The dentary presents three finger-like processes in its anterior ventral margin (seen in IHNFG 3004). The maxilla is thin and toothless. The premaxilla is triangular and bears a large tooth (previously observed in IHNFG 3004). There is a strong fang-like tooth in the palatine of IHNFG 2988.

The pelvic girdle is opposite to the origin of the dorsal fin. There are 10 dorsal and six anal fin rays. In IHNFG 2987 and IHNFG 2988 there are 35-37 total vertebrae, 14-15 of which are abdominal. The caudal peduncle is narrow. The caudal fin is wide, deeply forked, and its lobes are similar in size and shape. The body is naked except for the single mid-dorsal scute located just in front of the dorsal fin.

Remarks According to Silva (2007), there are about 26 - 27 *Enchodus* species that lived between the Barremian-Eocene range and had a wide geographical distribution all over North and South America, Africa, Europe, Middle East, and Asia. Five of these species occur in North American localities with ages between the Cenomanian and the Maastrichtian (Goody 1969; Fielitz 1996; Alvarado-Ortega et al. 2006a; Silva 2007). Unfortunately, these North American species are described mainly based on isolated and fragmentary material.

The specimens studied here are identified as *Enchodus* because they have the diagnostic characters of this genus described by Goody (1969) and Chalifa (1996). These characters are: a robust palatine with an anterior fang or hypertrophied tooth, three symphyseal finger-like processes on the anterior ventral margin of the dentary, and an uncovered lower jaw-quadrate joint (Figure 5).

TABLE 4. Comparison among the specimens described as *Enchodus* sp. in the present paper and those nominal species characterized by the occurrence of less than 40 total vertebrae that Chalifa (1996) included within her Cenomanian-Turonian group. Gray area shows shared characters.

	<i>Enchodus brevis</i>	<i>Enchodus</i> sp. (studied here)	<i>Enchodus marchesettii</i>	<i>Enchodus longipectoralis</i>
Total vertebrae	33	35-37	37	35
Abdominal vertebrae	10	14-15	13	19
Head length (as % of SL)	35	36.3	24.1	33.3

According to Chalifa (1996, tables 3 and 4), there is a Cenomanian-Turonian group of *Enchodus* species that is well characterized by the occurrence of less than 40 total vertebrae, and another group with younger species that shows more than 41. In this scenario, the Mexican *Enchodus* species described here match with the Cenomanian-Turonian group of *Enchodus* species that involves *E. marchesettii* (Kramberger 1895) (see Goody 1969, p. 85-95); *E. brevis* Chalifa 1989; and *E. longipectoralis* (Schaeffer 1947). Nevertheless, the Mexican *Enchodus* shows some singular characters that are summarized in Table 4, these are: the total number of vertebrae of this Mexican species (35-37) is similar to that found in *E. marchesettii* (37) and *E. longipectoralis* (35), it has 14-15 abdominal vertebra, unlike *E. marchesettii* and *E. longipectoralis* that have only 13 and 19, respectively (in contrast *E. brevis* has 33 total and 10 abdominal vertebra). In addition, the head length of this Mexican *Enchodus* species (36.3 % of the SL) is longer than that found in other species (it is 35 % in *E. brevis*, 33.3 % in *E. longipectoralis*, and 24.1 % in *E. marchesettii*). Although this brief analysis suggests that the *Enchodus* sp. from the Sierra Madre Formation represents a new form within the Cenomanian-Turonian group of *Enchodus* species described by Chalifa (1996), a complete descriptive and comparative analysis is required before suggesting a new nominal specific name.

Family Eurypholidae Goody, 1969
Genus *Saurorhamphus* Heckel, 1850
Saurorhamphus sp.

Type species: *Saurorhamphus freyeri* Heckel 1850, from lower Cenomanian of Comen, near Trieste, Slovenia.

Material examined – IHNFG 1916 a and b, IHNFG 2983, IHNFG 2667 a and b, and IHNFG 2982 a and b, from El Espinal quarry; IHNFG 2660 a and b, IHNFG 9084, and IHNFG 9130 from El Chango quarry (Figures 6.1-6.5).

Description – In IHNFG 2667, the most complete specimen so far known (Figure 6.4), the total and standard lengths are 305 and 265 mm, respectively. The head length is 127 mm (45 % of SL) and comprises three times its maximum depth. In IHNFG 2983 (Figure 6.1), the dorsal fin is 50 mm long; it is included three times in the trunk and is located in the anterior half. The anal fin is only 20 mm long; it is included eight times in the length of the trunk and is placed in the posterior quarter. The caudal fin is wide and deeply forked.

In IHNFG 2660, there are at least five mid-dorsal scutes located along the predorsal border, where they overlap (Figure 6.2-6.3). In these fishes there are about 38 total vertebrae, 17 abdominal plus 21 caudal (including both urals). The most anterior vertebrae are almost as twice as long as the posterior ones. In IHNFG 2982, there is a row of at least 37 scales along the flank of the trunk; the most anterior ones are located just above the spinal column but in the posterior part of the body, where these scales are covering the caudal vertebrae. Some of these anterior flank scales are disarticulated in IHNFG 2983 (Figure 6.1, 6.5) showing their rhomboidal shape and median ridge ornamented with tubercles and ridges [the shape of these scales was described as triangular by Goody (1969, p. 126) and illustrated by Chalifa (1985, p. 190, figure 3)].

Remarks – Goody (1969, p. 71, 191) named the suborder Enchodontoidae and included *Saurorhamphus* and the relatives of *Enchodus*. Among other characters, enchodontoids share the presence of an enlarged palatine tooth, scales are exclusively present along the lateral line of the body, there are scutes on the mid-dorsal line in front of the dorsal fin, and the spinal column has more caudal than abdominal centra. Although the palatine is obscured in all the specimens referred, they are included among enchodontoids because they have 21 caudal and 17 abdominal vertebrae, show scales on the lateral line of the body, and scutes in the mid-dorsal line (Figures 6).



FIGURE 6. *Saurorhamphus* sp. from Sierra Madre Formation. 1, IHNFG 2983, from El Espinal quarry. 2 and 3, IHNFG 2660, part and counterpart of the head of the same specimen from El Chango quarry. 4, IHNFG 2667 specimen from El Espinal quarry. 5, impression of a scale of IHNFG 2983, from the rectangle marked in 1. Abbreviations: af, anal fin; df, dorsal fin; dfr1, dorsal fin ray 1; lls, lateral line scales; mds, mid-dorsal scute; pop, preopercle; pvf, pelvic fin. Scale bars equal 50 mm.

According to Goody (1969), there are two enchodontoid families: his Eurypholidae, and Enchodontidae, firstly proposed by Woodward (1901). Although Chalifa (1985, p. 182) emended the diagnosis of the later family, she did not discuss the differences between both families; in consequence, we only consider the original diagnoses provided by Goody (1969). The diagnostic characters of eurypholids are: the articular facet of the

lower jaw is not visible in the lateral external view; the scales on the lateral line and the scutes on mid-dorsal line overlap; the preopercle bears a prominent posterior ventral spine; the opercle shows a posterior spine; and the ventral section of the cleithrum is expanded posteriorly, beyond the level in which the pelvic fin attaches to the body. The first three of these eurypholid characters are present in the Mexican *Saurorhamphus* specimens

TABLE 5. Comparison between the nominal *Saurorhamphus* species and the species from El Chango and El Espinal quarries herein studied (based on data from Goody 1969, Chalifa 1985, and Bannikov and Bacchia 2005). Gray areas show shared characters.

	<i>Saurorhamphus freyeri</i>	<i>Saurorhamphus judeaensis</i>	<i>Saurorhamphus giorgiae</i>	<i>Saurorhamphus</i> sp. (studied here)
Head length (as % of SL)	33	37-40	37	48
Dorsal fin origin into the trunk	In the posterior half			In the anterior half
Position of pelvic fin	Located closer to the pectoral fin than to the anal fin	Near the middle between pectoral and anal fin		Located closer to the anal fin than to the pectoral fin
Length of the anterior dorsal fin ray	Relatively short			Relatively long

referred here (Figure 6). In contrast, the diagnostic characters of the enchodontids are: the articular facet of lower jaw is visible in lateral external view, neither the scales on lateral line nor the scutes on the mid-dorsal line show overlapping, the preopercle and opercle do not bear posterior spines, and the ventral section of the cleithrum is not projected backward overhanging the pectoral fin.

Goody (1969) located *Eurypholis* Pictet 1850 and *Saurorhamphus* into his family, Eurypholidae. According to Gallo et al. (2005, p. 346, character 50), the scales of these fishes along the lateral line show a typical triangular shape (the shape of these scales is described here as rhomboidal). This diagnostic character is also present in the *Saurorhamphus* sp. from Chiapas (Figure 6.5).

According to Goody (1969), prognathism is less conspicuous in *Eurypholis* than in *Saurorhamphus*. *Eurypholis* has a pelvic fin located just behind the pectoral girdle, only three mid-dorsal scutes, about 35-40 total vertebrae, and 20 caudal vertebrae. In contrast, the spinal column of *Saurorhamphus* is markedly prognathic [the length of the head is more than three times as deep as the head]; it includes 42 and 22 total and caudal vertebrae, respectively; its pelvic fin is located in the middle of the abdomen (the position of the pelvic fin is variable in *Saurorhamphus* species, see Table 5) and has 6-8 scutes along the mid-dorsal border (Chalifa 1985). The inclusion of the specimens from Chiapas here referred as *Saurorhamphus* is supported because they share all these diagnostic characters except the total number of vertebrae (48).

Today the genus *Saurorhamphus* involves three nominal species, *S. freyeri* Heckel 1850, from Cenomanian deposits of Slovenia; *S. judeaensis* Chalifa 1985, from the Cenomanian limestones of

Ein-Yabrud, Near Jerusalem; and *S. giorgiae* Bannikov and Bacchia 2005, from Cenomanian deposits at Namoura, Lebanon. Based on a comparative study of the nominal species of *Saurorhamphus* performed by Chalifa (1985, table 3) and data provided by Bannikov and Bacchia (2005), four characters in the specimens from El Espinal and El Chango quarries are recognized that suggest they belong to a new species or probably to a new genus (Table 5). However, it is evident that a complete descriptive work of the Mexican *Saurorhamphus* is still required. These characters are:

1. The length of the body and that of the head are almost the same (the head length is 48 % of SL) in the Mexican specimens. In contrast, the head length is 33 % of SL in *Saurorhamphus freyeri*, it is 37 % of SL in *S. giorgiae*, and it ranges between 37 and 40 % of SL in *S. judeaensis* (see Chalifa 1985, tables 2, 3; Bannikov and Bacchia 2005, p. 518)
2. In the Mexican specimens, the dorsal fin is located in the anterior half of the SL, close to the skull (Figure 6.1). In contrast, all the nominal *Saurorhamphus* species show the dorsal fin located in the posterior half of the SL (see Bannikov and Bacchia 2005; Goody 1969, figure 55; Chalifa 1985, figure 3).
3. The anterior dorsal fin rays are hypertrophied in the Mexican specimens; here the length of the most anterior dorsal fin ray is equal to the length of five or six of its abdominal vertebrae (Figure 6.1). In contrast, the anterior dorsal fin ray in all the nominal *Saurorhamphus* species is markedly shorter; its length is contained in the length of one or two abdominal vertebrae (Goody 1969, figure 55; Chalifa 1985, figure 3E; Bannikov and Bacchia 2005, figure 3).

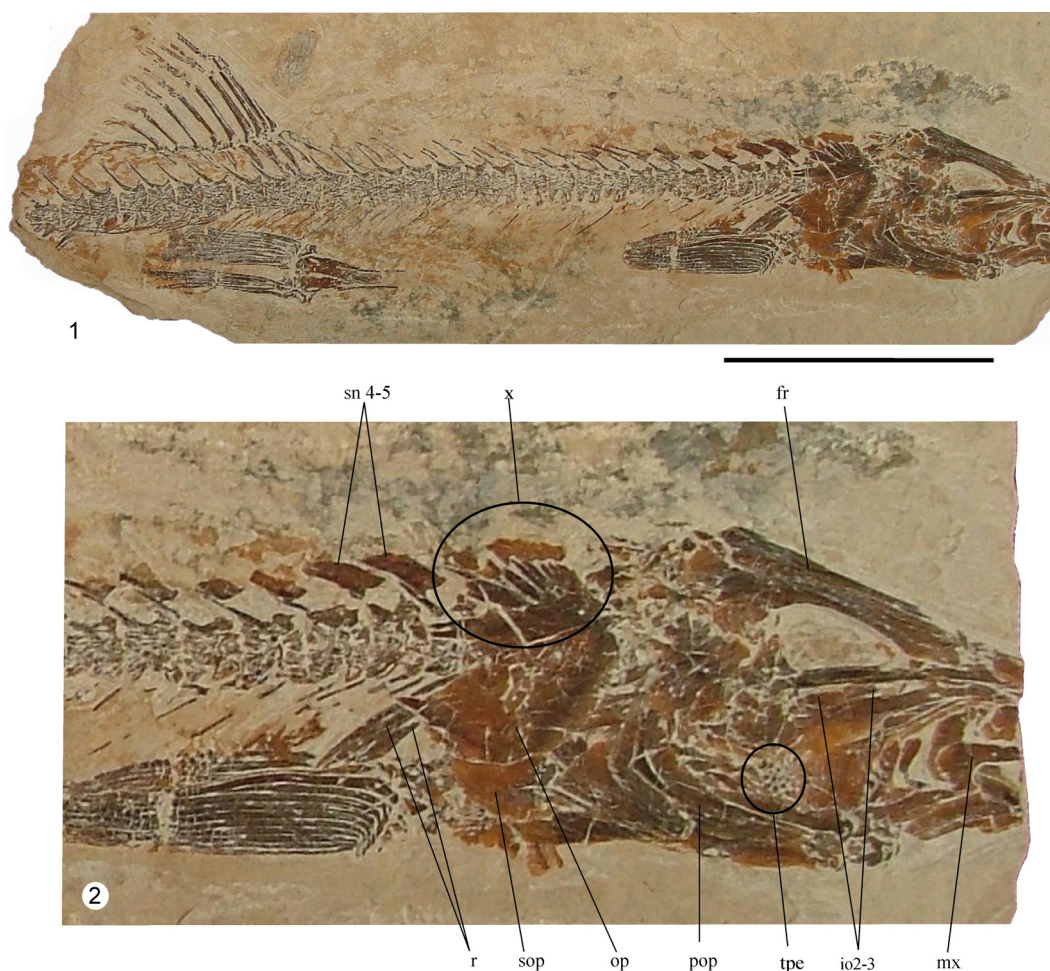


FIGURE 7. IHNFG 2986, a gonorhynchid fish from El Chango quarry. Abbreviations: fr, frontal; io 2-3, infraorbitals 2 and 3; mx, maxilla; op, opercle; pop, preopercle; r, ribs (first pair); sn 3-5, supraneurals 3–6; sop, subopercle; tpe, teeth patch on the endopterygoid; x, area in which the supraneurals 1-3 are in contact each other. Scale bars equal 30 mm.

4. The pelvic fin is placed in the posteriormost end in the Mexican specimens; it is behind the dorsal fin and closer to the anal fin base than to the pectoral fin (Figure 6.1). In contrast, the pelvic fin in *S. freyeri* and *S. judeaensis* is located in front of the dorsal fin and closer to the pectoral fin than to the anal fin base [in *S. freyi* it is located closest to the pectoral girdle (Chalifa 1985, table 3, figure 3E)], whereas in *S. giorgiae*, it is located right in the middle point between the pectoral and the anal fins (Bannikov and Bacchia 2005, figure 3).

Order Gonorynchiformes Greenwood, Rosen,
Weitzman, and Myers, 1966
Suborder Gonorynchoidei *sensu* Grande and Poyato-Ariza, 1999
Family Gonorynchidae *sensu* Grande and Poyato-

Ariza, 1999

Genus and species undetermined

Material examined – IHNFG 2986 (Figure 7) and IHNFG 2993 a and b, both from El Chango quarry.

Description – The bodies of the specimens referred here are incomplete, they lack the tail and IHNFG 2986 also lacks the anterior region of the skull (Figure 7). The specimen is a long fish with a narrow trunk and triangular head. The dorsal fin is located far from the occiput and opposite to the pelvic girdle. The neural arches and the first supraneurals are wide and in contact with each other (their position is named the X zone in Figure 7). The first rib is stout and wider than the posterior ones.

Remarks The presence of the Weberian apparatus characterizes the ostariophysan fishes (Fink and Fink 1981). This is a highly complex auditory sys-

tem constituted by modified vertebrae that connect the swim bladder with the ear (Greenwood et al. 1966). The temporal range of gonorynchiforms is from the Early Cretaceous to the present; they are considered the sister group of all other ostariophysans, because their Weberian apparatus represents a primitive condition in which the anterior neural arches are expanded in a lateral plane and the first pleural rib is expanded (Grande and Poyato-Ariza 1999). The specimens here referred are located in the order Gonorynchiformes because they show both diagnostic characters (Figure 7).

IHNFG 2986 (Figure 7) and IHNFG 2993 have characters that support their inclusion in the suborder Gonorynchoidei *sensu* Grande and Poyato-Ariza (1999). These characters are: the infraorbitals 2 and 3 are reduced; the supraneurals 1-3 are in contact with each other; and the supraneurals 3 and 4 are expanded. Besides, these authors recognized two gonorynchoid families, Gonorynchidae and Kneriidae. The specimens referred here show two synapomorphies of the family Gonorynchidae: the elongated frontals are narrow except in the postorbital region, and there is a patch of conical teeth on the endopterygoid (Figure 7). In addition, these specimens can be recognized as no-kneriids because they have supraneurals behind the fourth vertebra (the absence of supraneurals behind this vertebra is a synapomorphy of Kneriidae). A comprehensive comparative study of Gonorynchidae taxa including the specimens from Chiapas is required but it is beyond the scope of the present paper.

The gonorynchids are extinct, with exception of *Gonorynchus* Scopoli 1777, which lives in the Indian and Pacific oceans. Probably, all gonorynchids except *Notogoneus* Cope 1885 (collected in marine, as well as in presumably fresh and possibly brackish water deposits in Canada, USA, France, Germany, and England, see Grande and Grande 2008, p. 27) are marine fishes. The oldest record of gonorynchid fossils is from the Cenomanian marine localities in the Middle East (Lebanon and Israel) and Europe (Germany). In North America, gonorynchids have been collected in Campanian (Two Medicine Formation, Montana), Eocene (Green River Formation, Wyoming), and Paleocene (freshwater deposits of Alberta and Colorado) localities (see Wilson 1980, 1981; Grande and Grande 1999, 2008).

Before the present work, the gonorynchiform specimens found in Mexico were collected in two localities. A still undescribed gonorynchid was discovered in the Albian-Cenomanian marine sedi-

ment at Muhi quarry, Hidalgo (González-Rodríguez and Bravo-Cuevas 2005). At least two other gonorynchid forms have been recognized in the Albian fish assemblage from the Tlayúa quarry, Puebla; a large form reported by Applegate (1996) and a small one recently discovered (both fishes are under study by Núñez-Utrilla and Alvarado-Ortega) (Alvarado-Ortega and Núñez-Utrilla 2008). Regarding this scenario and the occurrence of gonorynchids within the Cenomanian deposits at El Chango quarry, Chiapas; it seems that the oldest gonorynchids so far known were diverse and well established in Mexico.

DISCUSSION

El Espinal and El Chango quarries are in the area where the Sierra Madre Formation crops out, as previously noted (see Ovalles-Damián and Alvarado-Ortega 2002; Ovalles-Damián et al. 2006; Vega et al. 2006, 2007). Nevertheless, no index fossil has been collected in these localities so far, preventing an accurate biostratigraphical correlation of these localities and the lithological zones recognized by Steele (1986) and Waite (1986), who performed a geological-paleontological study nearby these localities, about 10 km northwest from El Espinal quarry.

Vega et al. (2006, p. 324, 2007) suggested that El Espinal and El Chango strata correspond to “the lowermost lithofacies defined by Steele (1986, figure 4) and Waite (1986) as dolomite and dolomitic breccia (unit 1), located between 650 and 700 m from the base of the Sierra Madre Formation, which lies conformably over the Upper Jurassic–Lower Cretaceous San Ricardo Formation.” Nonetheless, Steele (1986) and Waite (1986) described their unit 1 as corresponding with the first 828-895 m of the Sierra Madre Formation sequence and suggested that it was deposited under supratidal or intertidal conditions. Unfortunately, these authors observed but did not sample the sections 400-748 m within this unit 1 and the whole unit 3 (which could be about 384 m thick). In this scenario, it is not possible to perform a proper comparison between El Espinal and El Chango strata with these non-sampled sections of the Sierra Madre Formation. Actually, additional research is required to determine the positions of El Espinal and El Chango strata within the Sierra Madre Formation.

Figure 8 summarizes the biostratigraphical ranges of the fossils from El Espinal and El Chango quarries identified by Vega et al. (2006, 2007) and the fishes described above. Although a

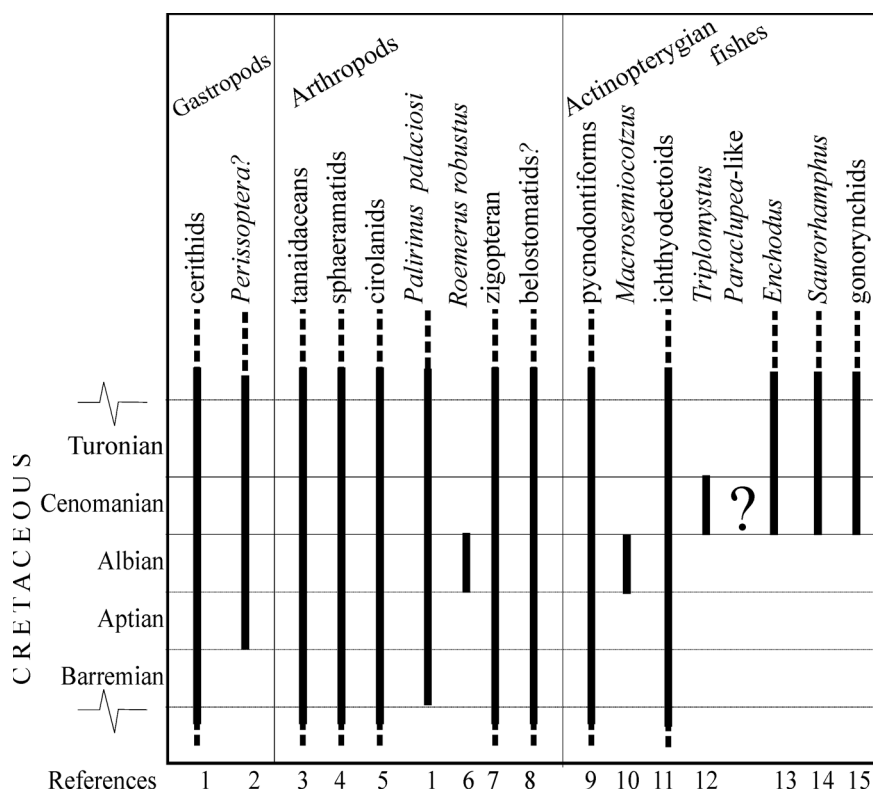


FIGURE 8. Biostratigraphical ranges of the fossil fauna assemblage as far identified in El Espinal and El Chango quarries. References: 1, Batten (1985); 2, Vega et al. (2006, 2007); 3, Knopf et al. (2006); 4, Brandt et al. (1999); 5, Wieder and Feldmann (1992); 6, Bishop (1983); 7, Wootton (1981); 8, Fraser et al. (1996); 9, Machado and Brito (2006); 10, González-Rodríguez et al. (2004); 11, Alvarado-Ortega (2005); 12, Forey et al. (2003); 13, Silva (2007); 14, Chalifa (1985); 15, Grande and Poyato-Ariza (1999).

detailed biostratigraphic analysis has not been performed to specify the age of the El Espinal and El Chango fossiliferous beds, the similarity of the Chiapas fossil assemblage and other Cenomanian localities from Europe and the Middle East makes it likely that the Chiapas fossils could have accumulated during the Cenomanian and not through the Albian as suggested by Vega et al. (2006, 2007). However, further analyses are necessary to confirm this hypothesis.

The fossil assemblage from El Espinal and El Chango quarries described by Vega et al. (2006, 2007) includes gastropods (cerithiids and probably a *Perissoptera* Tate 1865); crustaceans [tanaidaceans, isopods (Sphaeromatidae and Cirolanidae), and decapods (*Palirinus palaciosi* Vega, García-Barrera, Perrilliat, Coutiño, and Mariño-Pérez 2006; and *Roemerus robustus* Bishop 1983)], insects (an odonate-zygopteran nymph and a hemipteran-?belostomatid), as well as unidentified bivalves, echinoids (remains), ichnites, ostracods, and plant remains. *Perissoptera* is an Aptian-Campanian gastropod from Europe and North America (Saul 1998). Tanaidaceans have been a

defined group since the Carboniferous (Knopf et al. 2006). The cerithiid gastropods are an extant group that includes well-documented paleozoic species (Batten 1985). The sphaeromitid isopods are extant forms with a well-known Triassic record (Brandt et al. 1999); and unmistakable cirolanids appeared first in the Cretaceous, but their record must be older (Wieder and Feldman 1992). *Palirinus* occurs in sediments of Europe and Lebanon from upper Barremian- middle Eocene, but today this genus has a restricted distribution along the Eastern Atlantic Ocean, Mediterranean Sea, and off South East Africa (Palero and Abelló 2007). *Roemerus*, which only includes the species *R. robustus*, was firstly known and named based on specimens from the lower Albian of the Glen Rose Limestone, Texas (Bishop 1983). The range of zygoptera is Permian-recent (Wootton 1981). The oldest belostomatid known is from the Triassic (Fraser et al. 1996).

Vega et al. (2006, p. 324) wrote about El Espinal quarry that “similar fossils have been found at the Tlayúa Formation lithographic limestones of Albian age in Puebla.” Unfortunately, this proposi-

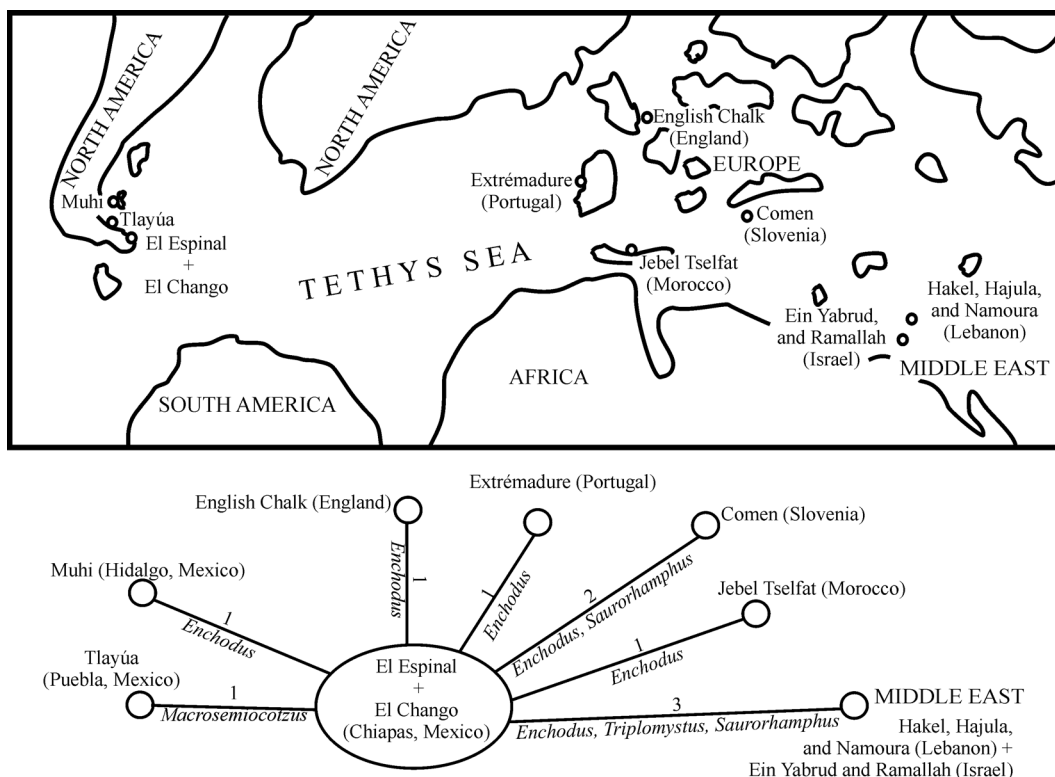


FIGURE 9. Biogeographical distribution of Cenomanian fossil fish assemblages in the Eastern and Western regions of the Tethys Sea (above), Tlayúa is an Albian age locality included only for comparative purposes). Common fossil fish genera found in El Espinal plus El Chango quarries and the other localities (below). Based on data from Forey et al. (2003), González-Rodríguez and Bravo-Cuevas (2005), Alvarado-Ortega (2005), and Applegate et al. (2006).

tion cannot be applied to fishes. Although these authors considered only the macrosemiid and the *Paraclupea*-like form referred here, which have closely related forms within the Tlayúa fish assemblage, there are hitherto more fishes to consider from Tlayúa, El Espinal, and El Chango quarries. Besides, unlike González-Rodríguez et al. (2002), who identified the macrosemiid from El Espinal as *Macrosemius fourneti*, a Jurassic (Kimmeridgian) species known from Cerin in France, we determine it as *Macrosemiocotzus*, a genus we described based on Albian specimens from Tlayúa. Ovalles-Damián (2004) described the *Paraclupea*-like taxon (considering that the order Ellimmichthyiformes is composed only of *Paraclupea*, *Ellimmichthys*, and *Diplomystus*), Zaragüeta-Bagils (2004) and Alvarado-Ortega et al. (2008) performed phylogenetic analyses of ellimmichthyiforms that suggest a more complex taxonomical composition of the group. Today, *Macrosemiocotzus* is the only fish common to Tlayúa and Sierra Madre formations.

Tlayúa quarry is located in Tepexi de Rodríguez, Puebla, Central Mexico. Often this

Albian Konservat-Lagerstätte locality is referred to as the “Mexican Solnhofen” due the extraordinary preservation, abundance, and biodiversity represented in the Tlayúa fossil assemblage (Alvarado-Ortega et al. 2007). Although the better represented fossils in Tlayúa are the fishes (Applegate 1996; Applegate et al. 2006; Alvarado-Ortega et al. 2006b; among others); a large part of taxa still require detailed taxonomic analysis. Based on the actual knowledge on the fossil fishes found in Tlayúa and El Espinal plus El Chango, the different composition of these assemblages is revealed.

Forey et al. (2003) provided a taxonomical list of the Cenomanian fishes of the Tethys Sea domains found in localities of Africa, Europe, and the Middle East. González-Rodríguez and Bravo-Cuevas (2005) provide similar information for the Albian-Cenomanian strata of the Muhi quarry, Hidalgo, Mexico. Recently, Alvarado-Ortega (2005) and Applegate et al. (2006) provided a general review of the Albian fossil fishes found in Tlayúa quarry. The comparison of these fish assemblages shows that *Enchodus* is present in two Mexican Cenomanian assemblages, El Espinal + El Chango

and Muhi, as well as in all the other localities except Tlayúa (Figure 9). Additionally, *Triplomystus* and *Saurorhamphus* are common genera in El Espinal + El Chango and localities from the Middle East.

A better taxonomic comparison between fishes from Mexican localities and other localities around the world requires much more detailed anatomical studies of the Mexican forms. Although El Espinal and El Chango quarries were deposited in the western part of the Tethys Sea, in contrast with the Cenomanian localities of Europe and Middle East (i.e., Comen, Namoura), which were deposited in the eastern part of the Tethys Sea, the fish assemblage of the former resembles those from the latter localities (Figure 9). This fact exposes the bias in our early knowledge on the temporal and geographical distribution and the systematic composition of certain fish groups in Mexico.

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